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Phenetic studies of African army ant queens of the genus *Dorylus* (Hymenoptera: Formicidae)

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ABSTRACT. Multivariate analyses of queens of fourteen species of the Old World army ant genus *Dorylus* were undertaken to assist in clarifying the status of the six included subgenera. Results were compared with two similar studies based on major workers and males, respectively. Queens are phenetically less divergent than either of the other two phena examined, although similar subgeneric relationships were observed. Taken together, these phenetic studies suggest that the subgenera *Rhogmus* and *Alaopone* are deserving of continued individual status, but that species of *Anomma* and *Dorylus* (s.s.) form one diverse taxon. A conservative classification would place *Dichthadia* and *Typhlopone* species together with the composite *Dorylus* (s.s.) – *Anomma* taxon.

Introduction

Species of the subfamily Dorylinae constitute the Old World army ants and are placed in the genera *Dorylus* and *Aenictus*. These two genera are distinguished morphologically from the New World army ants, or Ecitoninae, by an array of characters and are considered to have arisen independently of the New World forms. That is, the New and Old World army ants have evolved convergently the complex of morphological and behavioural characteristics used to define the true army ants (Gotwald, 1982). *Dorylus* and *Aenictus*, however, are as distinct from one another as either is from the Ecitoninae, and they themselves may represent separate but convergent evolutionary lines (Gotwald, 1979).

The Indo-Australian species of army ants are reasonably well known taxonomically, especially those belonging to *Dorylus*, since only four species of this genus are recorded from the region (Wilson, 1964). In Africa, however, these genera are poorly understood and were last treated taxonomically as a group by Emery (1910). In subsequent years, numerous descriptions of species, subspecies and varieties, most commonly of unassociated workers, males or queens, were added to the literature. As a result, each genus is a synonymic tangle of names. Both genera are being taxonomically revised by one of us (W.H.G.). This paper is a contribution to the revision of the genus *Dorylus*.

Dorylus is currently divided into six subgenera: *Alaopone*, *Anomma*, *Dichthadia*, *Dorylus*, *Rhogmus* and *Typhlopone*. The status of these subgenera must be determined within the context of the taxonomic revision, i.e. are these groups deserving of continued recognition, and if so, should they remain subgenera or be elevated to generic status? Although most of the subgenera can be distinguished easily from one another, there are no unambiguous characters that will

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separate *Dorylus* and *Anomma* from each other (Barr & Gotwald, 1982).

A series of phenetic studies was undertaken in an effort to clarify the status of the subgenera. The first of these studies examined the major workers (Gotwald & Barr, 1980), the second the males (Barr & Gotwald, 1982). Both studies provided support for the continued recognition of the subgeneric groupings corresponding to the current taxa *Alaopone*, *Rhogmus* and (less certainly) *Typhlopone*. The single species of *Dichthadia* included in both studies was found to be insufficiently distinct to warrant continued subgeneric status in a conservative classification. In both studies, moreover, species belonging to *Dorylus* and *Anomma* formed a mixed and loose association, a clear indication that they should be combined in a single taxon.

Of the three army ant phena, only the queen remains to be examined quantitatively, and this paper reports the results of an identical set of phenetic studies conducted on the queens. As noted previously (Barr & Gotwald, 1982), the value of such parallel studies lies not only in their contribution to narrow taxonomic objectives. Such investigations are also useful in demonstrating the extent of phenetic congruence between different phena belonging to the same set of taxa, making the results of heuristic value to evolutionary systematists. And when congruence between phena (or the lack of it) is incorporated into taxonomic decisions, the resulting classification will be of greater pragmatic value to practising taxonomists as well.

Materials and Methods

Methods used in this study, like those for males (Barr & Gotwald, 1982), were chosen to be consistent with, and thus comparable to, those described by Gotwald & Barr (1980), for major workers. In the earliest paper, the analytical techniques were discussed in more detail, and reasons were cited for the choice made.

A set of thirty-seven characters was used to describe the queens of each of the fourteen army ant species examined in the present study. Included in the set were metric,

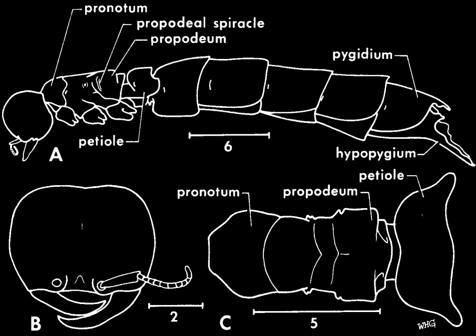

FIG. 1. Morphology of the queen of *Dorylus* (*Anomma*) sp. showing major features from which characters were drawn for the study. (A) Habitus, lateral view, legs and pilosity omitted. (B) Head, dorsal view, right antenna omitted. (C) Alitrunk (mesosoma) and petiole, dorsal view. Scales in mm.

meristic and ordered multistate characters as well as several standard myrmecological indices. *Dorylus* queens are dichthadiigynes, i.e. they possess a greatly enlarged petiole and gaster, are blind or nearly so, and are permanently apterous (Fig. 1). Although certain morphological features, e.g. the shape of the mandible, are rather homogeneous in appearance throughout the genus, other characters are of considerable taxonomic importance. Among these are the relative widths of the pronotum and propodeum, shape of the petiole, condition of the posterior margin of the pygidium (notched *v.* concave or straight), shape of the hypopygium, and position of the hypopygium relative to the pygidium (Figs. 1–3).

Army ant queens are relatively rare in collections, and so in addition to our previous reasons for using the exemplar method of characterizing species (Barr & Gotwald, 1982), we add the constraint of necessity. Fortunately, adherence to the exemplar technique throughout has made it possible to treat the queens of *Dorylus* spp. in a manner comparable to that used for males and major workers.

One complete analysis was carried out on the full set of raw data. Then, all metric characters in the data set were transformed to ratios of a standard size measure to reduce the influence of overall size in the resulting phenograms and ordinations. In previous studies on major workers and males, profemur length was chosen as the standard indicator of overall size. Unfortunately, the queen specimen representing species 2 in the present study was damaged and lacked both profemurs. Two variations in the analysis were attempted in order to compensate for the inadequate data. One set of computations was completed using data with metric characters transformed to ratios of mesofemur

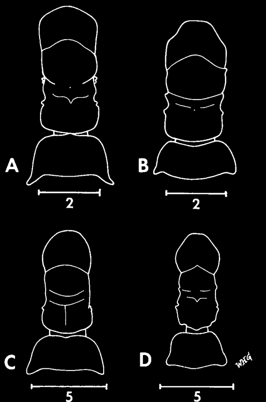

FIG. 2. Alitrunk and petiole of queens of the genus *Dorylus*, dorsal view. (A) *Alaopone*. (B) *Dorylus* (s.s.). (C) *Rhogmus*. (D) *Typhlopone*. Scales in mm.

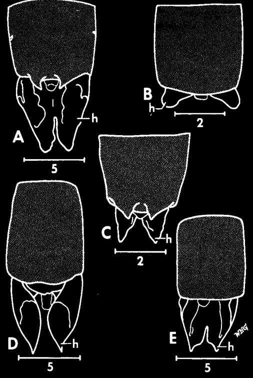

FIG. 3. Terminal abdominal segment of queens of the genus *Dorylus*, dorsal view. The pygidium is stippled, h = hypopygium. (A) *Anomma*. (B) *Alaopone*. (C) *Dorylus* (s.s.). (D) *Rhogmus*. (E) *Typhlopone*. Scales in mm.

length on the premise that this was an equally good indicator of overall size. The second strategy was to delete species 2 from the study and then analyse both the raw data and the data with metric characters transformed to ratios of profemur length for the thirteen-species set. The full character set is listed in the appendix, and those characters transformed to ratios are marked with an asterisk as noted. A complete set of raw scores for the thirty-seven-character data on each of fourteen species is available from any of the authors upon request.

Data for each of the full analyses described above were first standardized to deviations from the character mean in standard deviation units. The standardized data set was then used to calculate average taxonomic distance from each species to every other species, and also the product–moment correlation coefficients between all species. The unweighted pair-group method on averages (UPGMA) was used on both of these similarity measures to cluster species, and the results of clustering were plotted in the form of standard phenograms.

Standardized data also served as the basis for ordination procedures used to obtain a continuous view of species relationships, free of the arbitrary boundaries imposed by clustering techniques. Principal components analysis (PCA) was used to array the species of the study in three-dimensional attribute (A) space. Non-metric multidimensional scaling (MDS) on average taxonomic distances was also carried out, because its results are generally less affected by distortions which are inherent in PCA ordination. The MDS ordination was subsequently rotated to alignment with the major axes of variation established by PCA. A minimum spanning tree based on average taxonomic distances served as an objective check on the apparent clusters produced by the MDS analysis and to assist in visualizing any remaining distortion. The MDS results were plotted as three-dimensional diagrams so that similarity of relationships could be more readily assessed visually. All procedures are discussed by Sneath & Sokal (1973).

Computations were carried out on the IBM System 370/3033 computer at the University of Toronto. Clustering and ordination procedures were performed with the NTSYS package of programs (Rohlf *et al.*, 1972). Representation of ordinations in three-dimensional perspective was accomplished by the program PHYSETER written by Ralph Gibson at the University of Toronto.

Because synonymic details of the pending *Dorylus* revision have yet to be finalized, species included in this study are referred to only by number. Species numbers and the subgenera to which they belong are as follows: *Anomma* 1, 2, 3, 5 and 7; *Alaopone* 8 and 9; *Dorylus* (s.s.) 6, 10, 11, 12 and 13; *Rhogmus* 4; and *Typhlopone* 14.

Results

In this third study in the series, we have continued to use multivariate statistical procedures in the exploratory mode, as a tool for visualizing the inherent taxonomic structure in our data. Our goal here has been only to elucidate the relative phenetic affinities of the *Dorylus* species examined.

Gotwald & Barr (1980) discussed previously the reasons for believing that transformation of metric characters to ratios of a general size indicator provides the most reliable estimates of phenetic relationships. In addition, it was found in this study that analyses carried out on the thirteen-species set using profemur length to correct for size differences were the most reliable. That conclusion can be drawn from the following observations. In all analyses of the fourteen-species data set, species 1, 2 and 3 clustered tightly together, suggesting that species 2 is so similar to 1 and 3 that its phenetic position can always be inferred from the position of the other two. Moreover, analyses performed on the raw data for fourteen species are almost identical to those for the thirteen-species raw data set (with the exception only of the appearance of species 2 itself). Conversely, a comparison of the results from the thirteen-species set transformed first on profemur length and then on mesofemur length, showed many more differences than would be expected if both are equivalent indicators of overall size. Finally, restricting the conclusions of this study to analyses based on profemur transformations only is more clearly in keeping with our goal of maintaining consistency with previous work.

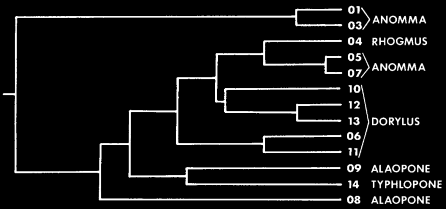

FIG. 4. Phenogram produced by UPGMA clustering of average taxonomic distances calculated on the thirteen-queen data set transformed by profemur length. Matrix correlation (cophenetic correlation) $r = 0.846$.

Thus, we will report here the results of analyses carried out on thirteen *Dorylus* queens, with metric characters transformed to ratios of profemur length. The affinities of species 2 will be assumed to be indicated accurately by the affinities of species 1 and 3, on the basis of the fourteen-species analyses not reported here in detail. Most of the species groups recognized in analyses of the transformed data were also present in similar results from the raw data, although inter-group relationships and placement of certain species varied.

Phenograms generated by the UPGMA technique on the thirteen-species set (raw data or profemur transformation) were similar in general features, and those illustrated in Figs. 4 and 5, based on the transformed data, are representative. The phenogram based on average taxonomic distances (Fig. 4) shows species 1 and 3 clustering separately from all other species. Within the second species group no compact clusters are seen, but rather a series of sequential linkages between four minor clusters. The identifiable species groups are: (i) species 4, 5 and 7, (ii) species 12 and 13, (iii) species 6 and 11, and (iv) species 9 and 14. These clusters mirror the subgeneric classification presently in use for this genus (Gotwald, 1982) only loosely. The subgenus *Anomma* is split into two distantly associated portions, and species in the subgenus *Dorylus* (s.s.), although occurring in

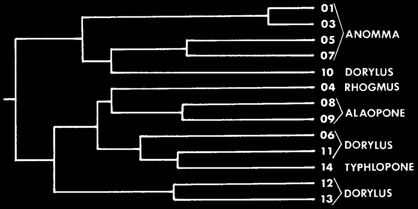

FIG. 5. Phenogram produced by UPGMA clustering of product–moment correlation coefficients calculated on the transformed data. Matrix correlation $r = 0.783$.

the same area of the phenogram, are only loosely associated. The single *Rhogmus* species is most closely associated with *Dorylus* (s.s.) and part of *Anomma*, but the two *Alaopone* species and the single *Typhlopone* species are well separated from the rest of the genus.

The phenogram based on correlation coefficients (Fig. 5) shows more distinct clusters than that based on distances and displays better correspondence with the existing classification. There are two major clusters, the first consisting of all species of *Anomma* with a single *Dorylus* (s.s.) species clustering with *Anomma* species 5 and 7. The second major cluster consists of widely dispersed *Dorylus* species associated loosely with the included species of *Rhogmus*, *Typhlopone* and *Alaopone*. A subcluster within this second group pairs the two *Alaopone* species and shows the single species of *Rhogmus* most closely associated with them.

In the belief that PCA analyses are somewhat less reliable than those from the MDS procedure, we utilized the former primarily as an aid to establishing the three most significant axes of variation, to determine the relative contribution of different characters to those first three principal component axes and as a seed for the MDS analysis. The first three component axes generated in the PCA procedure accounted for 64.2% of total variation in the transformed data set, a reduction from the 86.4% for the first three component axes in the analysis of raw data. The explanation for this reduction continues to lie (as described previously by Gotwald & Barr, 1980, and Barr & Gotwald, 1982) in the greatly reduced explanatory value of the first component axis (37.3% *v.* 67.1%) concordant with its change from being primarily an indicator of size differences to one of shape differences. Explanatory values for the second two axes actually increased for the transformed data.

In the transformed data set, principal component axis I was influenced most heavily (both positive and negative loadings) by characters expressing shape, either transformed lengths (distributed over all three body regions) or standard myrmecological shape indices. Body colour and absolute profemur length also made important contributions. Component axis II accounted for 16.7% of the variation in the data set. Of major significance for separating species in this dimension were relative size of several areas of the thorax, relative width of the first gastral segment, and the shape of the pygidium. Component axis III accounted for only 10.3% of the total variation and was strongly influenced only by the cephalic index, the relative metatibia length and the shape of the hypopygium.

Results of the MDS ordination are graphed in Fig. 6. Species are distributed widely through the attribute space, and few distinct clusters are evident. These are precisely the type of diffuse species relationships which produce the variable species groupings seen in

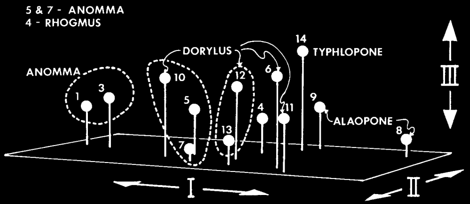

FIG. 6. Non-metric multidimensional scaling ordination of the thirteen *Dorylus* queens in the A space defined by the first three component axes (I, II, III), based on average taxonomic distances calculated on the transformed data (stress = 0.138). Matrix correlation $r = 0.969$.

the phenograms (Figs. 4 and 5). *Anomma* species 1 and 3 are paired and well separated from any other species, although their closest affinity is with *Anomma* species 5. The latter species is at the centre of a very diffuse cluster which also includes *Anomma* species 7 and all five *Dorylus* (s.s.) species in the study. The single species of *Rhogmus* also appears as part of this *Anomma–Dorylus* (s.s.) cluster, while the two species currently classified in *Alaopone* and the single *Typhlopone* species are at the same end of the attribute space but only loosely associated with the central swarm.

Discussion

Fig. 7 represents a schematic view of phenetic affinities of the queens of *Dorylus* species included in this study. It is based upon the MDS ordination and the results of clustering, with the minimum spanning tree of nearest-neighbour distances superimposed. Broken lines have been used to encircle species groups, defined in such a way that all nearest neighbour distances between circled groups exceed those among species within groups. Barr & Gotwald (1982) found this type of diagram the most useful aid in summarizing a suite of analyses such as those reported here.

On the basis of phenetic affinities of the *Dorylus* queens included in this study, a number of observations regarding subgeneric structure in the genus can be made. Species 1 and 3 (and, by inference, 2) currently placed in *Anomma* are closely related and distinct from the other species in the study. The remaining two *Anomma* species are loosely associated with the five species of *Dorylus* (s.s.) and the single *Rhogmus* species. No clear subgeneric breakdown is apparent within this group. Two of the *Dorylus* (s.s.) species (6 and 11) are also separated somewhat from the loose *Dorylus* (s.s.) – *Anomma* aggregation, but are less distinctive in position than the two *Anomma* species. Their position only serves to emphasize the diffuse structure of the cluster of species currently assigned to *Dorylus* (s.s.) and *Anomma*.

The single species now placed in the subgenus *Typhlopone* is related to the *Dorylus*

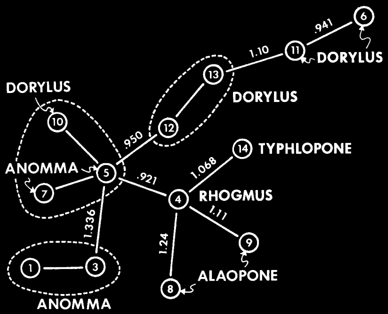

FIG. 7. Schematic representation of phenetic affinities of *Dorylus* spp. determined in the present study with the minimum spanning tree superimposed. Line lengths are in units of average taxonomic distance. Broken lines define species groups such that all exgroup nearest neighbour distances exceed those within groups.

(s.s.) – *Anomma* cluster through its association with *Rhogmus*. The two *Alaopone* species display a similar relationship but are not conspicuously closely associated with each other. It is of interest that these three species (8, 9 and 14) all show a closer relationship with the central cluster than either of the *Anomma* or *Dorylus* (s.s.) dissociated species pairs.

Were one to infer a subgeneric classification of African *Dorylus* species from phenetic studies of the queens alone, one would have to suggest that the genus shows no clear subgeneric boundaries, and that it is best treated as a homogeneous taxon of relatively similar species that, nevertheless, demonstrate varying affinities with one another. At the very least, it is clear that there is little distinction at the subgeneric level between species presently classified in the subgenus *Anomma* and those classified in the subgenus *Dorylus* (s.s.). Species representative of the other three subgenera included in this study could only be separated from the remainder of the genus by arbitrary decision.

We consider it inadvisable, however, to make sweeping taxonomic decisions based upon evidence from a single phenon. Thus, it seems appropriate at this point to compare the present study on *Dorylus* queens to previous work on the genus using the same techniques on data for major workers (Gotwald & Barr, 1980) and for males (Barr & Gotwald, 1982). Fig. 8 combines three schematic diagrams of the type appearing in Fig. 7 to facilitate comparison of the three studies.

Results from phenetic analyses of the three phena show a cline, from clear and distinctive, subgeneric-level groupings in the males, through increasing submergence of the subgenera *Typhlopone* and *Dichthadia* within the

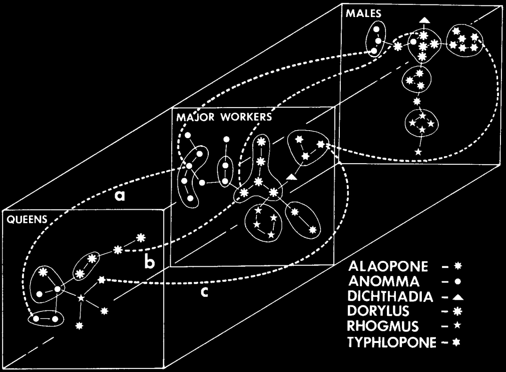

FIG. 8. Combined schematic diagrams like that of Fig. 7, for males, major workers and queens of the genus *Dorylus*. Species currently classified in each of the six subgenera are identified symbolically as indicated in the legend. Broken lines join the symbols for three species included in all three studies: (a) *Dorylus* (*Anomma*) *molestus* Gerstaecker, (b) *Dorylus* (s.s.) *affinis* Shuckard, (c) *Dorylus* (*Typhlopone*) *fulvus* Westwood.

group of species currently classified in *Dorylus* (s.s.). The final stage in this process is represented by phenetic affinities of the queens, where no clear subgeneric boundaries can be distinguished. Significantly, species presently classified in the subgenera *Anomma* and *Dorylus* (s.s.) are never clearly separable along classical subgeneric lines in any of the analyses reviewed here.

It may be hypothesized that the differences in phenetic distinctness of species among the three phena investigated are a consequence of the specialized features of army ant social organization (Gotwald, 1982). The entire life of a *Dorylus* queen is spent within the protective confinement of the colony. Workers, on the other hand, are involved in direct contact with the environment in foraging, colony maintenance and emigrating, although adherence to the army ant life style is rigid. Males, the only winged phase in the life history, leave the colony entirely and must survive outside its controlled environment. Apparently selective pressures for divergent adaptations are greatest in the males, less urgent for the major workers, and relatively mild in the queens. Males may, in addition (as noted by Barr & Gotwald, 1982), be subject to stronger pressures for divergence because of character displacement resulting from their sexually active role in seeking out queens to inseminate.

When arriving at a final decision on the subgeneric classification of the genus *Dorylus*, we advocate a relatively conservative philosophy. Not only must other factors such as cladistic hypotheses and practicality be considered when erecting a classification, but the results of the three phenetic studies (queens, major workers and males) must be reconciled. We will attempt the latter here.

Phenetic affinities of *Dorylus* males, queens and major workers are relatively consistent with one another (Fig. 8), with differences being attributable to varying degrees of coalescence of the classical subgeneric clusters. Even individual species followed throughout the three analyses occupy corresponding positions in the schematic diagrams. We take the view that the similarities among these three sets of results are more important than the differences. On this basis, it is clear that there is no support from phenetic studies for continued separate recognition of the subgenera *Anomma* and *Dorylus* (s.s.).

The species currently classified in *Dichthadia* and *Typhlopone* show close affinities, in general, with those of *Dorylus* (s.s.) and *Anomma*, and could probably be combined with them in a single, subgeneric-level taxon. Species of *Rhogmus* and *Alaopone*, on the other hand, maintain distinct clusters throughout most analyses and probably deserve continued ranking at the subgeneric level. The balance of available evidence suggests that these two species groups are no more closely related to each other than they are to the central *Dorylus* (s.s.) – *Anomma* cluster.

In summary, we recommend that at least three discrete species groups be recognized among African army ants currently classified in the genus *Dorylus*. These three groups correspond to species currently classified in the subgenera *Dorylus* (s.s.) (including *Anomma*, *Dichthadia* and *Typhlopone*), *Rhogmus* and *Alaopone*. Whether to recognize these groupings at the generic or subgeneric level must await the broader consideration which will be accorded the group in a complete revision.

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Appendix: Character list

(All lengths measured in millimetres to nearest 0.01 mm. Those characters transformed to ratios of profemur length for the analysis described in detail in the text are marked with an asterisk.) 1. Colour. *2. Length of terminal flagellar segment. *3. Length of second flagellar segment. *4. Scape length (excluding neck). *5. Scape index (SI), SL × 100/HW. *6. Head length. *7. Head width. 8. Cephalic index, HW × 100/HL. *9. Mandible length

(ML). 10. Mandibulocephalic index (MCI), ML x 100/HL. *11. Maximum mandible width (MMW). 12. Mandibular index (MI), MMW x 100/ML. *13. Head depth (HD), longest distance between occipital margin and anterior margin of head in lateral view. *14. Alitrunk length (AL), in lateral view. *15. Pronotum width. *16. Propodeum width, at and including protuberances of the propodeal spiracles. *17. Distance between the posterior borders of the pronotum and the propodeum measured along the midsagittal line. *18. Procoxa length. 19. Profemur length. *20. Protibia length. *21. Mesocoxa length. *22. Mesofemur length. *23. Mesotibia length. *24. Metacoxa length. *25. Metafemur length. *26. Metatibia length. *27. Petiole width. *28. Petiolar node length (PL). 29. Petiolar index (PI), PW x 100/PL. *30. Petiole height (PH), between dorsum and lateral margin of tergum in lateral view. *31. Length of petiole sternite along midsagittal line. *32. Maximum width of first gastral segment. *33. Length of first gastral segment sternite along midsagittal line. 34. Shape of posterior border of pygidium. 35. Shape of hypopygium in dorsal view. 36. Shape of hypopygium in lateral view. 37. Shape of distal margin of labrum.

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